PHYSIOLOGICAL STUDIES ON PLANARIA.

III. OXYGEN CONSUMPTION IN RELATION TO AGE (SIZE) DIFFERENCES.

L. H. HYMAN,

HULL ZOÖLOGICAL LABORATORY, UNIVERSITY OF CHICAGO.

I. REVIEW OF LITERATURE.

The present paper is a report of some determinations of the rate of oxygen consumption of small (young) as compared with large (old) planarians belonging to three different species. That the metabolic and other activities of small individuals are more rapid than those of large individuals of the same and different species is so well known from a number of independent investigations that further evidence appears almost superfluous. The majority of these investigations, however, deal with vertebrates, where a certain difficulty inherent in the nature of the material is encountered. This difficulty centers about the impossibility of finding a proper unit for comparison of animals of different sizes. Among the warm-blooded vertebrates, the metabolic rate has commonly been reckoned per unit of surface area on the necessity of taking into account loss of heat by radiation. But leaving out of consideration the difficulties of accurately measuring the surface, over which proceeding a controversy of long standing exists, the surface method of comparison is more or less meaningless in the case of cold-blooded animals. Nor is the method of comparison of metabolic rate per unit weight free from objection. A considerable part of the weight of the vertebrates and the higher invertebrates consists of skeletal material, connective tissue, fat, etc. The metabolic rate of such material must be relatively low, and further its proportion to the total weight must be different in animals of different sizes; nevertheless, these factors have not been considered in any of the researches on the subject, nor, as far as I am aware, has anyone

attempted to make a correction for these inert portions of the body.

As Benedict and Talbot ('14) concluded after a study of the metabolism of infants, metabolism cannot be accurately measured either by weight or by surface, but only by the amount of active protoplasm. It is probably impossible to determine this but certainly in the soft-bodied lower invertebrates, weight is a more accurate index of the amount of active protoplasm than is the case in higher forms, where skeleton is present. For this reason, the metabolism of the lower forms deserves more attention than it has hitherto received from physiologists.

Among the early investigators of the effect of size differences on metabolic rate were Jolyet and Regnard ('77), who determined the rate of oxygen consumption per unit weight of a large number of fish, and some of the higher invertebrates. They found that among related groups small species consume more oxygen per unit weight per unit time than large species; and small individuals more than large individuals of the same species. Vernon ('95) confirmed this conclusion. He measured the rate of oxygen consumption per unit weight of large and small individuals of the same species, using as material a hydrozoan medusa, a scyphozoan medusa, two ctenophores, two gasteropods, and two pelagic tunicates. With a few exceptions the smaller individuals were found to consume relatively more oxygen than the large ones. Bounhiol ('02) working with twelve species of polychæte annelids, belonging to several different families, found that the carbon dioxide production was greater the smaller the individual. This was true for individuals of the same and of different species. On the other hand, Montuori ('13) was unable to come to any definite conclusion from his measurements of the oxygen consumption of a large number of species belonging to most of the aquatic groups. In some cases the small individuals respired relatively faster than large ones of the same species; in others the reverse was found; and in still others there was no relation between size and rate of respiration. The great irregularity of Montuori's results, as well as their disagreement with the work of others, suggests that he failed to control adequately the conditions under which the experiments were performed. Child

('19) found that small individuals of *Planaria dorotocephala* produce more carbon dioxide per unit weight than large ones, and this experiment is now regularly performed as a class experiment. Allen ('19) has shown that the rate of oxygen consumption of *Planaria agilis* per unit weight is greater the smaller the animals, and reports that Miss Wolf working in the same laboratory found the same to be true for the leech, crayfish, branchipus, may-fly nymph, and stone-fly nymph. It is also the case with dragon-fly nymphs, as shown by Mr. G. C. Hawk in this laboratory. According to Morgulis ('15), the oxygen consumed per gram per hour by flounders is in general greater for small than for large animals. Tashiro and Adams ('14) note that the carbon-dioxide production of the ganglionic cord of the heart of *Limulus* is relatively greater in small than in large cords. Nicolas ('18) found that the young leaves and stems of plants give off from $3\frac{1}{2}$ to 7 times as much carbon-dioxide per gram per hour as old leaves and stems from the same branch.

A considerable amount of labor has been devoted to this problem in the case of mammals, especially man. Rubner originally maintained that warm-blooded animals of different sizes produce the same amount of heat per unit surface, but subsequent investigations have shown that this point of view is erroneous. Thus Magnus-Levy and Falk ('99) clearly showed that the oxygen consumption and carbon-dioxide production is highest in children and decreases with age, as measured either per unit weight or per unit surface. If individuals of the same size and weight but of different ages are compared, the younger ones respire the faster. The authors conclude that the protoplasm of children has a definitely higher rate of respiration per unit weight than that of mature individuals. References to other work supporting these conclusions will be found in their paper. Recently Du Bois ('16) and Gephart and Du Bois ('16) have verified this earlier work. The graphs and tables presented by Du Bois show that the heat production as measured per kilogram of weight is highest in infants and decreases gradually; as measured per unit of surface, it is low in infants, increases rapidly during the first year, reaches a maximum between the ages of 1 and 6, falls rapidly to 20, and thereafter

decreases more slowly. According to Benedict and Talbot ('14, '15), the metabolism of infants is about the same as that of adults, but the results were very variable. It seems highly probable that the metabolism of infants cannot properly be compared with that at other ages because: (1), the heat-regulating mechanisms of infants are known to be very imperfect; (2), infants commonly have relatively more fat than is present in normal individuals of other ages; and (3), the muscle tone of the voluntary muscles of infants must be lower than it is at other ages. Since a large part of the heat production of mammals originates in the voluntary muscles, this difference in muscle tone alone makes impossible any real comparison of the metabolism of infants with that of later stages of ontogeny when the muscles are in full use.

A few researches have been carried out on mammals other than man. Thus Slowtzoff ('03) working on dogs found that the oxygen consumption and carbon dioxide production per kilogram per minute is greater in small than in large individuals. A. V. and A. M. Hill ('13) determined the same relation in rats. Among birds, Bohr and Hasselbalch ('00) observed that the carbon dioxide production per kilogram per hour is considerably higher in newly hatched chicks than in the adult hen.

These researches are sufficiently numerous to establish the generalization that smaller (younger) individuals have a higher metabolic rate than larger (older) ones. The investigations on man clearly show that the difference is due to age and not to size. Age is also probably the determining factor in the metabolic difference found between large and small species, since, in general, species which grow to a large size must be older by the time they have attained that size than are adult individuals of small species.

How far back in the ontogeny can this generalization be carried? At what point in the ontogeny does the metabolic rate attain its highest value? Few researches have been carried out upon these points. The eggs of animals are probably cells of very low metabolic rate. After fertilization, the metabolic rate gradually rises, as development proceeds, up to a certain point and then falls. In the sea-urchin egg (*Arbacia punctulata*),

the oxygen consumption was found to rise continuously up through late cleavage (determinations stopped at this point); and in the eggs of *Fundulus heteroclitus*, up to the time when the embryonic axis is established after which it fell, rising again later apparently as the result of functional activity (unpublished personal observations). Unfortunately in these cases, nothing is known of the metabolic rate of the adult. Hasselbalch ('00) and Bohr and Hasselbalch ('00) have measured the rate of carbon dioxide production and oxygen consumption per kilogram in chick embryos. Both were found to be very high in the earliest stages determined—five or six days,—much higher than those of the adult; the rates then fell rapidly. The carbon dioxide output fell to the ninth day, after which it was about contant, and about equal to that of the adult. The oxygen consumption fell to the eleventh day, then rose again, and on the sixteenth day was again considerably higher than that of the adult. Bohr ('00) compared the carbon-dioxide output of guinea-pig embryos with that of the mother. He did this by cutting open the uterus under anæsthesia, determining the carbon-dioxide output of the mother and fœtuses, then clamping the umbilical cords of the fœtuses, and again measuring the CO_2 output of the mother. The difference between the two measurements supposedly represents the carbon-dioxide production due to the embryos. Of the six experiments of this kind performed by Bohr, five showed the carbon-dioxide production of the fœtuses to be greater than that of the mother. The case where the youngest embryos (5.5 grs. each) were encountered gave a carbon-dioxide output very much higher than that of the mother; the next size (16.5 grs. each) gave less CO_2, but still at a rate considerably higher than that of the mother; while in the other four cases, with large fœtuses, the CO_2 production was slightly higher than that of the mother in three, lower in one.[1]

[1] I wish to state that the conclusions which I have drawn after careful perusal of the papers of Bohr and Hasselbalch are somewhat different from those stated by the authors. They conclude, curiously enough, that the respiratory rate of the embryos of the hen and guinea pig is no higher than that of the adult, and anyone reading their conclusion alone would certainly be misled. The authors have either overlooked or ignored the fact, which their experimental data clearly show,

These researches indicate that the rate of respiratory exchange is very high at some certain stage in the embryonic development, this stage probably differing in different animals, and falls subsequently. Later it probably rises with increased functional activity. It certainly seems to me that the metabolic rate of embryos, especially vertebrate embryos, cannot vaildly be compared with that of post-embryonic stages, owing to the enormous differences in functional activity which exist between two such stages. The comparison of the metabolic rate of a chick embryo with an adult hen seems to me a simple absurdity when one reflects upon the difference in muscle tension alone at the two stages. The fact that the total metabolic rate of chick embryos was at no stage found to be less than that of the hen, certainly indicates that if cells of the same degree of functional activity could be compared in embryo and adult, the metabolic rate of the embryonic cells would be vastly the greater. The same criticism applies to cases where the young remain more or less helpless after birth or hatching.

In addition to these researches in which direct measurement of the rate of oxygen consumption or carbon dioxide output of young and old animals have been made, a considerable mass of data is available in which another method was employed. This is the direct susceptibility method extensively used in this laboratory by Child and others; it consists in observing the time of death of organisms in lethal solutions of various substances. We have brought forward a large amount of evidence[1] to indicate that the time of death in such solutions is an index of metabolic rate, individuals of higher metabolic rate dying first. When individuals of different ages are compared by this method, it is invariably found that the time of death is shorter the younger the individual, *always providing that the same degree of functional activity is present in the animals which are being*

that the rate of respiratory exchange in the youngest embryos with which they dealt very greatly exceeds that of the adult. It is only at certain later stages that the rates of the two are approximately equal. The authors seem to have an idea that the rate of respiratory exchange ought to be the same throughout development, whereas their own and other data show that it is high in early stages and declines as development proceeds. This decline is probably of the same nature as that which organisms undergo from birth to maturity.

[1] A general résumé of this evidence will be found in Child, '13.

compared. This age difference in susceptibility to toxic solutions has been observed in *Paramecium*, three species of *Hydra*, a number of colonial hydroids and hydromedusæ, several species of planarians, and several small aquatic oligochætes; and the rise in metabolic rate which is a feature of early development has also been demonstrated by this method.

Not only does the rate of respiratory exchange in organisms vary inversely with age but many physiological activities exhibit the same relation. Bert ('70) was among the first to observe this fact. He noted that the rate of respiratory movements is faster in small than in large individuals of the same and related species. Ducceschi ('03) studied the rate of movement of the fins, tail, fin membrane, and operculum of a large number of fish of different sizes; the rate of movement of the maxillipeds, abdominal appendages, and claws of several crustacea; and of the fins and mantle of some cephalopods; and found that it varies inversely as the size of the animal. Mayer ('06) and Child ('18) observed that the rate of contraction of the bells of medusæ is faster the smaller the animal. The number of respiratory movements per minute of *Octopus* is greater the smaller the individual (Polimanti, '13). In four species of sea-cucumber, Crozier ('16) observed that the pulsation of the cloaca is more rapid the smaller the animal. Hecht ('16, '18) noted that small Ascidia pass relatively more water through their siphons than large ones; and further that the rate of the heart beat in Ascidia varies inversely as the size of the animal. In man, of course, it is well known that the rate of the heart beat is fastest in the fœtus and decreases progressively with age. The rate of growth follows a similar law.

The results of the present experiments are in full accord with those of previous investigators. Small (young) planarians whether asexually or sexually produced, consume more oxygen per unit weight per unit time than large (old) ones.

II. Experiments with *Planaria dorotocephala*.

Planaria dorotocephala lives in spring-fed marshes in morainic regions near Chicago. It has never been found sexually mature in nature (although sexual maturity has been experimentally

induced by Dr. Child in this laboratory), but maintains itself by means of asexual fission. In fission, the posterior portion of the body pulls away from the anterior end, regenerates a head and becomes a complete small worm. Such small worms correspond in all tests which have been made upon them, to young worms in species reproducing sexually.

Six experiments were performed in which the rate of oxygen consumption of such small worms, under 10 mm. in length, was compared with that of large worms, over 20 mm. in length. In all cases, both large and small individuals were taken from the same stock and had been kept under the same conditions previous to the experiment. No worms showing signs of recent fission or regeneration were used. The heads were cut off the day before the test was made in order to eliminate movement. Two successive determinations of the oxygen consumption of each lot of worms were usually made, the worms were then weighed, and the oxygen consumption per two hours per 0.5 grams weight then calculated.

The method of determining the rate of oxygen consumption and the method of weighing have been described in previous papers (Hyman, '19*a*, '19*b*).

The results of the six experiments are given in Table I. In all cases the smaller worms consume more oxygen per unit weight per unit time than the larger ones. The per cent. difference ranges from 18 to 55, and closer inspection of the table reveals that the amount of difference is correlated with the length of time which has elapsed since the last feeding. In experiment 4, where the small worms respire but 18 per cent. more than the large ones, only two days had elapsed since feeding, while in the other experiments, where three or four days had passed since feeding, the difference is greater. As shown in a preceding paper (Hyman, '19*b*), feeding greatly increases the rate of oxygen consumption by stimulating the digestive tract. Since the digestive tract is more extensive in large than in small individuals, the difference between such individuals is decreased by feeding. As I did not perform any experiments with worms deprived of food for longer than four days, I do not know whether further starvation would increase the difference between small and large

TABLE I.

COMPARISON OF THE RATE OF OXYGEN CONSUMPTION OF LARGE (OVER 20 MM.) AND SMALL (UNDER 10 MM.) INDIVIDUALS OF *Planaria dorotocephala.*

Size of Worm.	C.c. Oxygen Consumed in 2 Hours.	Weight in Grams.	Oxygen Consumed by 0.5 Grs. in 2 Hours.	Per Cent. Difference.
Exp. 1. Worms Collected March 12, Last Fed April 2, Tested April 5. Temp. 22.5° C.				
Large	0.18 0.20	0.316	0.30	
Small	0.24 0.29	0.325	0.40	33
Exp. 2. Worms Collected March 12, Last Fed March 14, Tested March 17. Temp. 22° C.				
Large	0.12 0.11	0.187	0.30	
Small	0.23 0.17	0.255	0.39	30
Exp. 3. Worms Collected Early Winter, Last Fed April 23, Tested April 26. Temp. 21° C.				
Large	0.09 0.08	0.179	0.23	
Small	0.14 0.13	0.216	0.31	48
Exp. 4. Worms Collected March 12, Last Fed April 30, Tested May 2. Temp. 21° C.				
Large	0.16 0.17	0.160	0.51	
Small	0.22 0.24	0.192	0.59	18
Exp. 5. Worms from Mixed Stock, Last Fed May 6, Tested May 10. Temp. 21° C.				
Large	0.13 0.12	0.146	0.42	
Small	0.17 0.15	0.123	0.65	55
Exp. 6. Worms Collected May 28, Last Fed June 6, Tested June 10. Temp. 22° C.				
Large	0.33	0.370	0.22	
Small	0.33	0.272	0.31	41

worms, but it is scarcely likely since the effect of feeding has almost completely disappeared in four days. In Allen's experiments (Allen, '19) with *Planaria agilis*, worms starved 27 days were used, and in that case the difference between the largest

and smallest worms was about 40 per cent. (Table I., decapitated worms).

III. Experiments with *Planaria velata*.

Planaria velata lives in the Chicago region in temporary ponds, usually those that are passing into prairie, known to ecologists as "prairie ponds." Like the preceding species it is never found sexually mature, and reproduces exclusively by a peculiar asexual method. After the worms have attained a certain size, pieces drop off from the posterior end, surround themselves with mucus, and pass into an encysted condition. This process continues until the entire worm has formed a series of cysts. Within the cysts, the pieces undergo regeneration into complete worms of very small size, and these emerge from the cysts in about four weeks. This cycle is repeated as long as the ponds contain water; after the water dries up, the cysts remain quiescent until the following spring.

Table II.

Comparison of the Rate of Oxygen Consumption of Large and Small Individuals of *Planaria velata*.

	C.c. Oxygen Consumed in 2 Hours.	Weight in Grams.	Oxygen Consumed by 0.5 Grs. in 2 Hours.
Three Lots of Worms 10–12 mm. Long, before Encystment; Collected March 7, Last Fed March 10, Tested 13. Temp. 22° C.			
Lot *C*	0.42 0.52	0.745	0.31
Lot *D*	0.58 0.52	0.774	0.35
Lot *E*	0.41	0.593	0.34
Three Lots of Worms less than 4 mm. Long, Emerged during May from Cysts Formed by Above Lots of Worms; Fed Several Times after Emergence; Last Feeding June 6, Tested June 9. Temp. 22° C.			
Lot *C*	0.16 0.16	0.125	0.64
Lot *D*	0.16 0.16	0.127	0.63
Lot *E*	0.10 0.09	0.070	0.67

Owing to the nature of the life cycle of this animal, it was not possible to test the large and small worms simultaneously but the large worms were tested before encystment, the small ones after

emerging from the cysts. Three lots of each size were used. The worms were all taken from the same stock. The results are given in Table II. The heads were not removed in these cases, since the worms were also used for another experiment.

The table shows that the small worms consume 100 per cent. more oxygen than the large worms. The greater difference in this case than with the preceding species is probably due to the greater reorganization involved in the production of young worms with this species. As shown in another paper (Hyman, '19*c*), the process of regeneration of itself brings about a great increase in the rate of oxygen consumption.

IV. Experiments with *Planaria maculata*.

The so-called species *Planaria maculata* lives in the eastern United States under stones in ponds and in the Chicago region on submersed vegetation. It is highly probable that these two are not the same species as *Planaria maculata* from the Chicago region has never been found sexually mature, while that from Massachusetts is sexually mature and lays capsules all summer long; further the behavior of the two in regeneration is quite distinct. The forms used in this experiment were collected from a pond at Falmouth, Mass., and the experiments were performed at the Marine Biological Laboratory, Woods Hole, Mass., I am indebted to the director, Professor F. R. Lillie, for a research room in this laboratory.

Sexually mature worms, young worms, and egg capsules were collected at Falmouth and brought to Woods Hole. The rate of oxygen consumption of the mature worms was tested with one exception soon after they were collected. The young worms collected, together with those which subsequently emerged from the capsules, were kept for some time and fed at short intervals on liver (mostly fish liver) until a considerable number of them were at hand, whereupon their rate of oxygen consumption was determined. In all cases the heads were removed at least several hours before the test.

The results are recorded in Table III. The young worms consume about 50 per cent. more oxygen than the sexually mature individuals.

Table III.

Comparison of the Rate of Oxygen Consumption of Sexually Mature Individuals (15 Mm. or Longer) with the Sexually Produced Young (5 Mm. or Less) of *Planaria maculata.*

No. of Lot.	C.c. Oxygen Consumed in Test.	Weight in Grams.	Oxygen Consumed. by 0.5 Grams in 2 Hours.
Four Lots of Sexually Mature Individuals, Collected July 10; First Three Lots Tested July 11; Fourth Lot Kept Until August 11, with Frequent Feedings, Last Feeding August 8, Tested August 11. Temp. 20° C.			
Lot 1	0.30 in 2 0.31 hours	0.700	0.21
Lot 2	0.32 0.32	0.677	0.23
Lot 3	0.30 0.26	0.680	0.20
Lot 4	0.09 0.07	0.152	0.17
Three Lots of Sexually Produced Young; Young and Capsules Collected July 10 Fed at Frequent Intervals; Last Feeding of Lots 1 and 2, July 28, Tested July 31; Lot 3, Last Feeding August 8, Tested August 11. Temp. 20° C.			
Lot 1	0.14 in 3 0.12 hours	0.101	0.32
Lot 2	0.11 0.11	0.091	0.32
Lot 3	0.16 0.18	0.117	0.28

V. Conclusions.

These experiments show that small or young planarians consume oxygen at a faster rate per unit weight than larger or older ones. As already stated, the carbon dioxide production is also inversely proportional to the size of the worms. It is true that experiments of this kind do not and cannot prove that the protoplasm of young animals actually has an intrinsically higher metabolic rate than that of older ones, for the reason that it is impossible to discover what part of the weight of an animal is active protoplasm and what part inert material. Nevertheless there cannot be any reasonable doubt that the metabolic rate is inversely proportional to age. It would be difficult to suggest any other explanation for many of the facts cited in this paper. namely, for the faster rate of respiration, faster heart beat, and more rapid rate of other physiological activities of young as

compared with older organisms. The fact further that the susceptibility of young animals to a number of toxic substances is greater than that of old could scarcely be supposed to be due to a greater percentage of inert materials in the older individuals,

An interesting point brought out in these experiments is that the difference between the asexual and the sexual young and their respective adults is of about the same magnitude, when considered the same length of time after feeding. Worms produced by fission are therefore as truly "young" as those which develop from the egg.

In previous papers of this series (Hyman, '19*b*, '19*c*), it was shown that planarians which have been starved seven or eight weeks and pieces of planaria which have undergone regeneration have a much higher rate of oxygen consumption than ordinary fed worms, all tests being made, of course, a few days after feeding. Starved, regenerated and young worms therefore have this physiological characteristic in common: their metabolic rate is higher than that of large fed worms. That of starved ones is highest, regenerated ones next, and young, when produced from the egg or simple fission, least. It therefore appears that the metabolic rate of reduced forms depends primarily upon the amount of reorganization involved in their production, and is proportional to the degree of reorganization which has taken place. As a further illustration of this may be cited the much higher metabolic rate of the asexual young of *Planaria velata* than those of *P. dorotocephala*, presumably because much more extensive changes are involved in giving rise to the former. The evidence presented in these papers clearly supports the view which has been long maintained by Child—that such reorganizations due to whatever cause are rejuvenating transformations, restoring the organism to a physiological condition resembling that of the young.

V. Summary.

1. The young of *Planaria dorotocephala* produced by simple fission were found to consume 15 to 55 per cent. more oxygen than large worms, the difference depending upon the length of time which had elapsed between the last feeding and the time of testing.

2. The young of *Planaria velata*, produced by an asexual process involving regeneration and a high degree of reorganization of the body, consume about 100 per cent. more oxygen than the worms from which they come. The greater difference in this species is undoubtedly associated with the method by which the young are produced.

3. The sexually produced young of *Planaria maculata* consume about 50 per cent. more oxygen than the sexually mature worms. There is thus no significant difference between sexual and asexual young, when the latter arise by ordinary simple fission.

4. This result, that young worms have a higher metabolic rate than old ones, is in accord with a considerable body of literature on other forms leading to the same conclusion; and confirms the work previously done in this laboratory upon this same point by other methods.

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